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Source: *The Journal of Wildlife Management*, Vol. 62, No. 4 (Oct., 1998), pp. 1359-1372

Published by: [Wiley](#) on behalf of the [Wildlife Society](#)

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DENSITY AND FORAGING ECOLOGY OF WOODPECKERS FOLLOWING A STAND-REPLACEMENT FIRE

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Abstract: Throughout its geographic range, the black-backed woodpecker (*Picoides arcticus*) is rare and appears very similar in its foraging ecology to 2 broadly sympatric congeners, the three-toed (*P. tridactylus*) and hairy woodpecker (*P. villosus*). The purposes of our study were to test for differences in foraging ecology of the black-backed, three-toed, and hairy woodpeckers following a stand-replacement fire and to evaluate the importance of such fires to the viability of populations of the black-backed woodpecker. In boreal forests of Interior Alaska, endemic population densities of three-toed woodpeckers are low (<0.1/ha), and black-backed woodpeckers are extremely rare. Following the Rosie Creek fire near Fairbanks, Alaska, in June 1983, both species increased markedly. Densities of both species briefly exceeded 0.2/ha and remained high in a 67-ha plot at the edge of the burn during the following 2 years. By December 1986, densities had declined to <0.1/ha. Black-backed woodpeckers fed primarily on charred portions of moderately to heavily burnt spruces and almost exclusively by excavating larval wood-boring beetles (Cerambycidae). Three-toed woodpeckers fed on less-burnt spruces and foraged in and immediately under the bark; bark beetle (Scolytidae) larvae predominated in their diet. In contrast to earlier studies, our results demonstrate substantive differences in foraging sites, behavior, and diet of these 2 species. Foraging ecology of male hairy woodpeckers and black-backed woodpeckers, particularly females, was similar. In all 3 species, particularly the hairy woodpecker, females fed lower on trees and were far less numerous than males in the study area, which suggested intersexual displacement from foraging sites and habitats selected by males. In summer 1985, following initial adult emergence of the 1983 cerambycid and scolytid cohorts, woodpeckers declined markedly and were absent by late spring 1986. Our results suggest the black-backed woodpecker is extremely specialized in its foraging niche, exploiting outbreaks of wood-boring beetles in dying conifers for only 2–3 years after fires. Consequently, this species may be particularly vulnerable to local and regional extinction as fire suppression intensifies and programs of intensive salvage logging are pursued following fires.

JOURNAL OF WILDLIFE MANAGEMENT 62(4):1359–1372

Key words: black-backed woodpecker, fire, foraging, hairy woodpecker, *Picoides arcticus*, *Picoides tridactylus*, *Picoides villosus*, salvage logging, three-toed woodpecker.

Foraging niches of sympatric insectivorous birds typically are well differentiated (MacArthur 1958, Cody 1974, Richman and Price 1992), particularly among woodpeckers (Williams and Batzli 1979, Török 1990). Furthermore, sexual differences in foraging ecology are pronounced and associated with strong dimorphism in bill length in both the three-toed woodpecker in Eurasia (Hogstad 1976) and the hairy woodpecker in North America (Kilham 1965, Selander 1965, Morrison and With 1987). In less sexually dimorphic woodpeckers, either males exclude females from their territories, except during breeding when mated pairs share territories (Hogstad 1978), or males share territories with females throughout the year but

competitively displace them from mutually preferred foraging microhabitats (Peters and Grubb 1983, Matthysen et al. 1991). Such studies have supported the long-standing notion of limiting similarity: if food is limiting, coexistence is possible only if there are sufficient differences in morphology and behavior for partitioning use of resources (also see Wallace 1974, Pimm and Pimm 1982).

Broad overlaps in geographic ranges (Bent 1939, Bock and Bock 1974), habitat use (Bull et al. 1986), foraging behavior (Short 1974, Bull et al. 1986, Villard and Beninger 1993; but also see Villard 1994), and food habits (Beal 1911, Kilham 1965) of black-backed, three-toed, and hairy woodpeckers seem to contradict general theories of coexistence of closely related species. However, both theoretical treatments (Connell 1978, Huston 1979) and field studies (Rabenold 1978, Rotenberry and Wiens 1980)

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have emphasized that coexistence could be facilitated by disturbances of sufficient frequency and intensity to override the potential influence of interspecific competition in determining presence and relative abundance of potentially competing species. Woodpeckers, including black-backed, three-toed, and hairy woodpeckers, are well known to respond opportunistically to insect outbreaks following fires in coniferous forests (Bent 1939, Blackford 1955, Mayfield 1958, Koplin 1969, Heinselman 1973, Apfelbaum and Haney 1981, Hutto 1995). Perhaps these woodpeckers coexist despite greatly overlapping foraging niches because they exploit superabundant but ephemeral resources. Alternatively, they may differ more in their foraging niches than studies to date have suggested.

The Rosie Creek fire near Fairbanks, Alaska, in June 1983 provided us with the opportunity to compare the foraging ecology of black-backed, three-toed, and hairy woodpeckers, as all 3 species were seen there in abundance as early as August 1983 and remained common to abundant the next few years, particularly on the perimeter of the burn. Our results support Hutto's (1995) conclusion that the black-backed woodpecker is likely dependent on availability of standing dead forests created by stand-replacement fires, which suggests that salvage logging following fires may eliminate critical habitat for this species.

STUDY AREA

The Rosie Creek fire began accidentally on 29 May 1983, when a resident left a burning pile of brush unattended near the Tanana River, about 30 km west of Fairbanks. The fire spread quickly westward through forest stands of white spruce (*Picea glauca*), aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) in uplands, and black spruce (*Picea mariana*) and tamarack (*Larix laricina*) in boggy lowlands. The fire was temporarily controlled by 1 June, but on 2 June the fire escaped control at its western edge, becoming a firestorm for several hours. By 3 June, the fire had consumed about 3,500 ha, when rainfall and suppression efforts effectively controlled further spread (Juday 1985). Although the fire was anthropogenic, it occurred at the same time of year that lightning-ignited fires peak in boreal forests (Rowe and Scotter 1973, Viereck 1973, Flannigan and Wotton 1991), and thus its effects probably closely mimicked those of natural fire. By Sep-

tember 1983, woodpeckers were seen in abundance in fire-damaged white spruce stands on the edge of the burn (D. D. Gibson, University of Alaska Museum, personal communication).

Our study area encompassed the perimeter of the burn along its upper edge, in an area dominated by mature white spruce. There are 4 resident and 1 migrant species of woodpeckers that could occur in the study area. The only migrant, the northern flicker (*Colaptes auratus*), uses a variety of habitats (Gabrielson and Lincoln 1959, Spindler and Kessel 1980), and the downy woodpecker (*Picoides pubescens*) is most prevalent in deciduous woods. Neither species was common in the study area during our study; for example, we observed only 4 flickers and 3 downy woodpeckers during surveys (see below); hence, we do not consider these 2 species further. The 3 other species of the genus *Picoides*, the black-backed, three-toed, and hairy woodpeckers, thus became the focus of our study. Both the three-toed and hairy woodpecker likely occurred in low numbers in the study area before the fire (see Spindler and Kessel 1980), but the black-backed woodpecker, which is extremely rare in Alaska (Gabrielson and Lincoln 1959), probably was absent.

METHODS

Counts of Woodpeckers

Following preliminary observations during the 1983–84 winter, which indicated woodpeckers were concentrated on the upper edge of the burn, we established a single 67-ha plot for surveying and observing woodpeckers. The plot contained roughly equal areas of burned and unburned sections of forest and was centered on the edge of the burn. The plot encompassed most of a single research reserve where no salvage logging or reforestation projects were scheduled (Juday 1985); all other areas of the burn were scheduled for salvage logging, which precluded establishment of replicate plots elsewhere in the burn or along its perimeter. We established 67 100-m² subplots. To survey woodpeckers, we used a modified fixed-plot method (Amman and Baldwin 1960, Otvos 1965), stopping at the center point of each subplot to record all woodpeckers seen or heard within the subplot for a 4-min period and then walking quickly to an adjacent center point to minimize double-counting of individuals.

In the first 3 surveys, we found the entire plot could not be surveyed in the several hours that woodpeckers were actively foraging each morning; thus, we surveyed only 43 subplots. Subsequently, we surveyed this 43-ha "upper" section and the remaining 24-ha "lower" section on different days, typically surveying the lower section 1 day (maximum = 9 days) after the upper section. We began surveying woodpeckers on the upper section on 31 July 1984 and the lower section on 4 October 1984. From then until 4–5 December 1986, we conducted paired surveys ($n = 16$) of the upper and lower sections once every 1–2 months. Count totals reported below for "all woodpeckers" include individuals unidentified to species. For the first 3 surveys, when only the upper section was surveyed, we estimated numbers on the lower section, using the overall ratio of counts on the 2 sections for the remaining 6 surveys in 1984–85 (when both sections were surveyed) to make those results comparable with all later surveys.

Behavioral Observations of Woodpeckers

We located woodpeckers opportunistically for behavioral observations by walking through the study area, looking and listening for birds. Once a bird was found, it was observed until it flew out of view. For each foraging substrate where we observed a woodpecker, we recorded species (spruce, birch, aspen), height (if standing), circumference at breast height (if standing), and a burn severity index: (1) unburned, (2) burned at base only and slowly dying, (3) burned above base but less than half of the height of the trunk, (4) more than half burned, and (5) totally burned. We categorized substrate status as either standing or on the ground.

For each woodpecker we observed foraging, we recorded species, sex (when possible), height on the tree when observations started or the bird alighted ("initial height"), height on the tree immediately before its departure ("final height"), and duration of the observation. We estimated all heights based on the tape-measured distance between the observer and the tree and the slope between the observer and the base of the tree. We used a Spiegel-relaskop to measure the angles from the observer to the base and top of the tree and initial and final heights of foraging woodpeckers. We later used trigonometric functions to estimate all height variables. Using initial and final heights and duration of the observation, we calculated net dis-

tance moved (virtually all focal woodpeckers only moved upward). We categorized observations as "entire," if the bird was observed both landing and departing, or "partial," if the bird already was on the substrate when observations began.

We recorded the bird's foraging behavior once every 30 sec (initially once each minute). Following Conner (1979), we categorized foraging behaviors as flaking (hitting the bark of the tree with a glancing blow of the bill to make bark chips fly off), pecking (making slow blows perpendicularly to the tree trunk; i.e., directly into the bark), or excavating (making repeated hard blows at approximately the same point into the bark of the tree, resulting in a hole through the bark and often into the cambium or sapwood).

Behavioral observations began on 21 June 1984, about 1 year after the fire, and continued through 24 April 1986. During this period, observations were conducted on 38 days, on 1 or more days in most months. The total time spent actually observing foraging individuals was 22.3 hr for black-backed, 19.0 hr for three-toed, and 3.1 hr for hairy woodpeckers.

Collections

We collected specimens of all 3 species opportunistically on 6 days during early- to late-morning hours between 14 September 1984 and 6 October 1986. We made the collections on the perimeter of the burn, about 10 km east of our study site, where habitat structure and burn severity were similar; we stopped collections once salvage logging started at this site. We only collected foraging individuals. We preserved stomach contents in 70% ethanol. G. C. Stevens (University of New Mexico) identified prey remains to taxonomic levels we report below.

Statistical Analysis

In statistical analyses, we separately examined intersexual and interspecific differences in foraging substrates and behaviors because (1) differences between sexes could be pronounced but variable among species (e.g., Hogstad 1993), and (2) we sometimes could determine species but not sex of the bird we were observing. Thus, we tested separately for sex differences within species and for overall differences among species. Because we made 3 separate tests for sex differences, 1 for each species, we

used a Bonferroni adjustment of the P -value, testing for significance at $P = 0.013$ instead of $P = 0.05$. For nominal scale variables (tree species, substrate type), we computed log-likelihood ratio (G) test statistics. For ordinal (burn severity) and all ratio-scale variables (which frequently were not normally distributed within samples), we conducted Mann-Whitney tests for sex differences (with Bonferroni adjustments as above) and Kruskal-Wallis tests for differences among species, following each significant Kruskal-Wallis test with Tukey's pairwise comparison procedure. Because males of each species substantially outnumbered females in our samples (see below), we also conducted interspecific comparisons with only males. These comparisons included a 2-way analysis of variance (ANOVA) on ranked data (see Conover 1980) to test for effects of species, year, and a species \times year interaction on burn severity of foraging substrates.

RESULTS

Numbers of Woodpeckers

Although no surveys were conducted in the study area before the fire, results of other studies of bird communities in upland spruce habitats in the region (e.g., Spindler and Kessel 1980) suggested densities of three-toed and hairy woodpeckers were likely low, and the black-backed woodpecker was absent in the study area before the fire. In the first winter following the fire (1983–84), we noted that woodpeckers, particularly black-backed and three-toed woodpeckers, were abundant in the burn, especially on its upland perimeter. Our first quantitative surveys were on 31 July 1984, slightly >1 year after the fire. During that summer and the following winter (1984–85), black-backed woodpeckers generally were common on the study plot (Fig. 1); the maximum count was 17 on 31 October 1984. The black-backed woodpecker was common until late 1985; however, it was rare throughout 1986 and had vacated the area by early 1987, in the fourth winter following the fire. In 1987 and all later years, neither we nor any birders specifically looking for black-backed woodpeckers (e.g., J. C. Haney, The Wilderness Society, personal communication) observed the species during several visits to the survey plot and nearby areas. Overall, males constituted 75% of our sightings of this species.

Three-toed woodpeckers were common to abundant in the second winter after the fire: the maximum count was 16 on both 27 September and 29 November 1984. They were much less common in the 1985–86 winter, the third winter after the fire, and we only rarely observed them in late 1986 (Fig. 1). We recorded females infrequently compared to males (10% of sightings). Although we searched for this species in areas adjacent to the study plot, we rarely found female three-toed woodpeckers during our study; thus, females occurred only rarely in areas and habitats where males initially were abundant and then common for 3 years after the fire.

Hairy woodpeckers were more abundant in our initial surveys 1 summer after the fire than subsequently (Fig. 1). The peak estimate was 13 on 3 August 1984. After summer 1984, numbers generally were low except in midsummer 1985, when 8 were recorded. We recorded males much more often than females; overall, males constituted 81% of the survey sample.

Numbers of woodpeckers of each species in the survey plot declined through the course of our study (product-moment correlations between numbers and date; all P s < 0.05). Peak densities of woodpeckers of all species combined were about 0.5/ha (no. counted/67 ha) in fall 1984 (Fig. 1). Total numbers of woodpeckers declined throughout our study ($r = -0.59$, $P = 0.002$, $n = 19$; Fig. 1).

Foraging Habitats

Almost all sightings of all 3 species were on spruces. However, only 62% of female hairy woodpecker sightings were on spruce (Table 1); consequently, differences among species were highly significant (log-likelihood ratio test, $G_2 = 18.651$, $P < 0.001$). There were no differences between females and males within species (Table 1) or among species ($G_2 = 2.892$, $P = 0.235$) in status (standing vs. down) of foraging substrates; most individuals fed on standing trees.

There were clear and highly significant differences among species in burn severity of foraging substrates (Table 1; ANOVA on ranks, species effect: $F_{2,285} = 47.37$, $P < 0.001$). On average, three-toed woodpeckers selected lightly to moderately burned trees, black-backed woodpeckers selected moderately to heavily burned trees, and hairy woodpeckers selected heavily burned trees. Within species, we categorized burn severity index for too few female

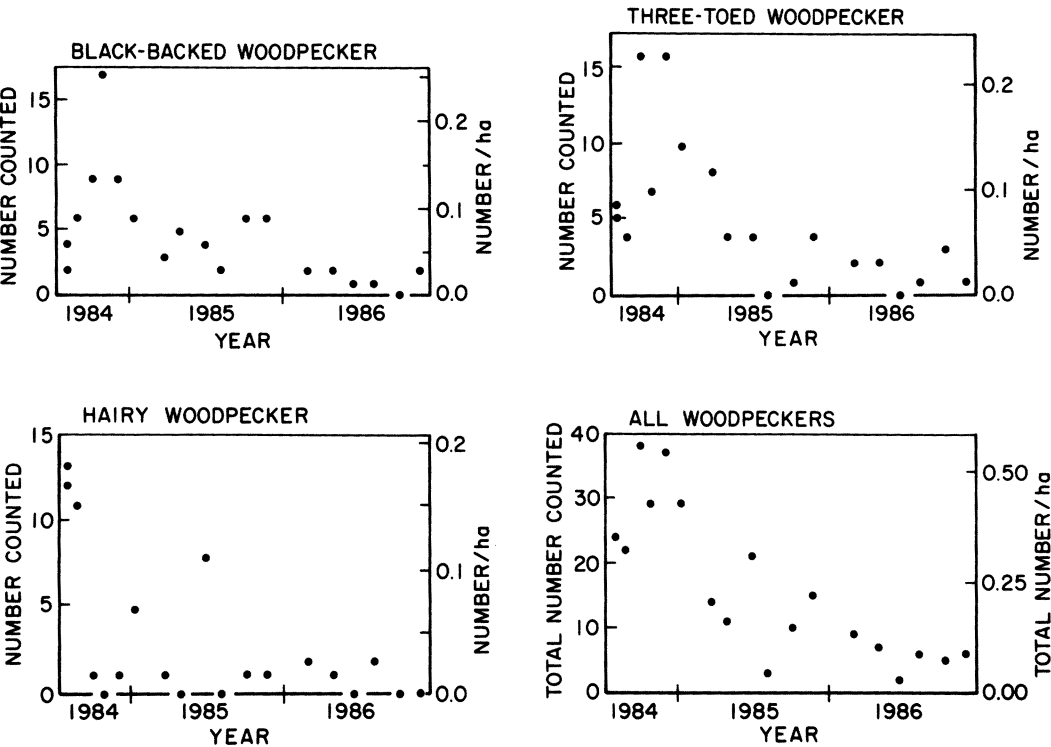


Fig. 1. Counts of woodpeckers in the study plot on the edge of Rosie Creek burn, July 1984–April 1986; “all woodpeckers” includes individuals not identified to species. Note that our first 3 surveys covered only the 43-ha “upper section.” The numbers we report for those surveys are estimates for the entire 67-ha plot, based on counts in the 43-ha upper section on those dates and the relative numbers on the 43-ha upper section and 24-ha lower section on the next 6 surveys of the entire plot.

Table 1. Characteristics of foraging sites of woodpeckers in Rosie Creek burn, June 1984–April 1986.

Species Sex	<i>n</i> ^b	Spruce (%)	Standing (%)	Burn severity index ^a			Tree height (m)			Circumference of tree (cm)		
				\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>
Black-backed woodpecker												
Male	134	97.8	94.8	3.2	0.1	140	24.7	0.7	129	114.3	2.9	132
Female	41	100.0	97.6	3.7	0.1	55*	26.2	1.2	40	109.9	4.8	40
All ^c	206	98.5	96.1	3.4	0.1	234	25.4	0.5	200	115.7	2.4	203
Three-toed woodpecker												
Male	81	91.4	96.3	2.5	0.1	114	26.4	0.9	77	133.4	3.7	80
Female	12	100.0	100.0	2.9	0.3	16	23.0	2.0	12	108.8	12.3	12*
All ^c	118	93.2	97.5	2.5	0.1	163	27.3	1.0	114	130.4	3.1	117
Hairy woodpecker												
Male	41	95.0	90.0	3.9	1.1	37	22.8	8.5	36	112	29	37
Female	13	61.5*	100.0	3.2	1.1	5	26.1	5.1	11	122	27	11
All ^c	63	83.6	91.8	3.9	1.0	50	23.3	7.9	54	113	30	56

^a Burn severity index is coded as follows: 1 = unburned, 2 = burned as base only and slowly dying, 3 = burned above base but less than half of the height of the trunk, 4 = more than half burned, and 5 = totally burned.

^b Sample size is the total number of behavioral bouts observed; sample sizes for particular variables are lower if data on those variables were not collected during 1 or more observations. Note that sample sizes for burn severity index typically exceed those for behavioral observations because we recorded burn severity index for trees where we observed birds during surveys as well.

^c Includes individuals whose sex could not be determined.

* $P < 0.0133$ (Bonferroni adjustment) of null hypothesis of no difference between males and females within a species.

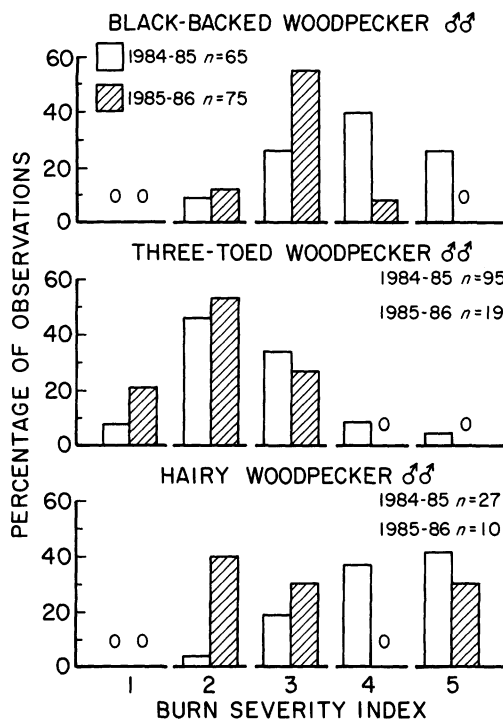


Fig. 2. Frequency distributions of male black-backed, three-toed, and hairy woodpeckers in relation to severity of burning of foraging trees. Burn severity index is coded as (1) unburned, (2) burned at base only and slowly dying, (3) burned above base but less than half the height of the trunk, (4) more than half burned, or (5) totally burned.

three-toed and hairy woodpeckers for meaningful comparisons, but female black-backed woodpeckers fed on more heavily burned trees than did males (Table 1).

We recorded burn severity index of foraging substrates for many more males than females of all 3 species, particularly in 1985–86. Limiting the analysis to only males, we conducted a 2-factor ANOVA on ranked values, grouping by species and year (1984–85: 1 Jul 1984–30 Jun 1985; 1985–86: 1 Jul 1985–30 Jun 1986). The species effect was highly significant ($P < 0.001$), paralleling overall results in Table 1. The year effect also was highly significant ($P < 0.001$), indicating males of all 3 species fed on less-burnt substrates in 1985–86 than in 1984–85 (Fig. 2). The species \times year interaction was marginally significant ($P = 0.051$), reflecting the greater shift between years to less-burnt trees by male black-backed and hairy woodpeckers than by three-toed woodpeckers.

There were no differences either among species (ANOVA on ranks, $P = 0.068$) or between males and females in the heights of trees where

we observed foraging individuals (Table 1). Male three-toed woodpeckers fed on trees of greater circumference than females (Table 1) and black-backed and hairy woodpeckers of both sexes (ANOVA on ranks, species effect: $F_{2,272} = 8.26$, $P < 0.001$; Tukey's pairwise comparisons, $P < 0.05$).

Foraging Behaviors

Preliminary analysis indicated no difference (ANOVA, bout-type effect: $P > 0.30$) in initial foraging heights of woodpeckers that we observed flying to trees or already foraging on trees. Therefore, we used all observations to test for species and sex differences in initial heights of foraging bouts. There were no differences among species ($P = 0.133$), but, on average, males started their foraging bouts lower on trees than females (Table 2), and the difference between sexes was highly significant for black-backed woodpeckers ($P < 0.001$). Final heights (points of departure) on trees showed the same pattern (Table 2). Neither duration nor movement rate varied among species ($P = 0.561$ and $P = 0.886$, respectively) or between males and females of the same species (Table 2).

We recorded only 3 foraging modes (flake, peck, excavate) during our study. We observed few female three-toed woodpeckers foraging in both seasons and no female black-backed or hairy woodpeckers foraging in 1985–86. Foraging mode varied markedly among species ($G_4 = 233.01$, $P < 0.001$). Male three-toed woodpeckers excavated relatively infrequently (27.6% of 853 observations) compared to both male black-backed (60.0%; $n = 1,109$) and hairy (70.7%; $n = 82$) woodpeckers. Three-toed males predominantly pecked (55.7%; $n = 853$).

We observed sufficient numbers of foraging behaviors of both male ($n = 358$) and female ($n = 154$) black-backed woodpeckers in 1984–85 to test for sexual differences in foraging mode: there were none ($G_2 = 3.85$, $P = 0.15$). In 1984–85, we also recorded 47 foraging observations for male hairy woodpeckers and 18 for females. Differences between sexes were significant ($G_2 = 9.52$, $P = 0.009$): females were pecking on 55.6% and excavating on only 44.4% of the observations, while males primarily excavated (72.3% of observations).

To examine between-year variability in foraging modes, we initially conducted a log-likelihood analysis of a 3-dimensional contingency

Table 2. Locations and movement rates of foraging woodpeckers in Rosie Creek burn, June 1984–April 1986.

Species Sex	Initial height (m)			Final height (m)			Duration ^a (min)			Movement rate (m/min)		
	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>
Black-backed woodpecker												
Male	8.1	0.5	119	10.6	0.6	113	5.85	1.59	50	0.79	0.10	106
Female	12.8	1.2	39**	15.2	1.3	40**	3.78	1.07	23	0.78	0.14	39
All ^b	10.3	0.5	189	12.8	0.5	183	4.52	0.97	87	0.92	0.10	175
Three-toed woodpecker												
Male	6.9	0.7	73	11.2	0.8	74	4.56	1.73	25	0.86	0.14	70
Female	11.3	2.1	12	15.5	2.3	10	1.38	0.56	4	1.19	0.47	9
All ^b	8.9	0.6	108	12.7	0.7	107	3.97	1.28	35	0.96	0.12	100
Hairy woodpecker												
Male	8.7	6.9	34	9.7	7.1	33	2.22	4.61	14	1.46	1.80	30
Female	12.8	5.8	11	14.4	4.5	8	6.95	5.30	5	1.56	1.71	8
All ^b	10.2	6.8	51	11.2	6.8	47	2.90	4.58	25	1.35	1.70	44

^a Duration reported only for complete behavioral bouts (times recorded when bird arrived on the substrate and when bird departed).

^b Included individuals whose sex could not be determined.

* $P < 0.013$, ** $P < 0.0013$ (H_0 : No difference between males and females).

table (grouping by species, year, and foraging mode) for males only and found that no reduced model provided an adequate fit to the data. We then ran the same analysis, omitting male three-toed woodpeckers. In this analysis, the year \times foraging mode interaction term improved the model ($P < 0.05$), but the species \times foraging mode term did not. Thus, male black-backed and hairy woodpeckers foraged similarly overall (both predominately excavated), but both excavated more in 1984–85 than in 1985–86 (black-backed: 64.5% in 1984–85 and 57.8% in 1985–86; hairy: 72.3% in 1984–85 and 68.6%

in 1985–86). Male black-backed woodpeckers were observed pecking relatively more in 1985–86 (33.0% of observations) than in 1984–85 (25.7%), and male hairy woodpeckers were observed flaking relatively more in 1985–86 (17.1%) than in 1984–85 (8.5%).

For male three-toed woodpeckers, pecking constituted 51.1% of foraging observations in 1984–85 and 77.3% in 1985–86. Excavating constituted 31.6% of observations in 1984–85 and only 8.7% in 1985–86. The differences between three-toed and both black-backed and hairy males were marked: male three-toed woodpeckers excavated much less than did male black-backed (and hairy) woodpeckers, and the percentage excavating declined between 1984–85 and 1985–86 (Fig. 3). In recording foraging mode, we did not differentiate between superficial excavating (to the cambium) and deeper excavating (into the sapwood), but all 248 “excavations” of three-toed woodpeckers were superficial and only penetrated to the cambium, not the sapwood (i.e., we never observed three-toed woodpeckers removing chips of sapwood). In contrast, we frequently observed both black-backed and hairy males excavating wood.

Food Habits

D. D. Gibson (University of Alaska Museum) collected 2 black-backed woodpeckers on 3 September 1983 and found their stomachs contained cerambycid and scolytid beetle remains. We collected 13 black-backed woodpeckers; all were feeding on charred substrates on spruces, in accord with our observations of this species in our primary study area. Analysis of stomach

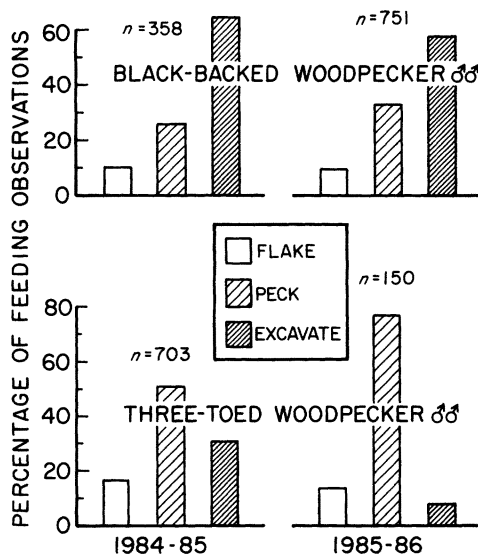


Fig. 3. Relative frequencies of foraging modes of black-backed and three-toed woodpeckers (males only), Rosie Creek burn, June 1984–April 1986.

Table 3. Numbers of prey items (frequency of occurrence) in stomach samples of woodpeckers, Rosie Creek burn.

Species	n	Prey taxon								
		Cerambycidae			Scolytidae			Other ^a		
		\bar{x}	SE	Range	\bar{x}	SE	Range	\bar{x}	SE	Range
Black-backed	13	16.6	4.6	(4–62) ^b	0.1	0.1	(0–1)	0.7	0.0	(0–3)
Three-toed	18	20.3	9.5	(0–171)	42.7	10.2	(0–144)	1.2	0.8	(0–14)
Hairy	2	(6–9) ^b			0			(2–3)		

^a Includes other Coleoptera (Buprestidae, Carabidae, Elateridae), other insects (Dermaptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera), other arthropods (Arachnida, Chilopoda), and unidentified plant seeds.

^b Range (minimum–maximum).

contents showed they were feeding primarily on wood-boring beetle larvae (predominantly Cerambycidae; see Table 3). In contrast, the 11 male three-toed woodpeckers we collected had been feeding mostly on bark beetles (Scolytidae) and only on wood-boring beetle larvae that were still in the cambium (first instar). We collected only 2 female three-toed woodpeckers in the second and third years after the fire, again indicating they were foraging in other habitat types away from the perimeter of the burn. We observed numerous female three-toed woodpeckers only in October 1986 (the fourth autumn after the fire), when we searched unburned forests near the edge of the burn; we collected 5, and all were feeding heavily on the bark beetle *Phloesinus pini* and first-instar larvae of an unidentified cerambycid on branches in the canopies of live spruces. On that day, we observed few male three-toed woodpeckers, and no black-backed woodpeckers, in that area or in our usual collecting area.

DISCUSSION

Foraging Ecology of Woodpeckers

Our analyses of foods suggest black-backed woodpeckers specialized on the larvae of wood-boring beetles, particularly the white-spotted sawyer (*Monochamus scutellatus*), a long-horned beetle (also see Blackford 1955, Wickman 1965, Villard and Beninger 1993). Larvae of this species grow to substantial size (to 50 mm) before emerging 2–3 years later as adults. The white-spotted sawyer was by far the most abundant wood-borer in our study area, and oviposition sites and larval survival were highest on charred portions of moderately burned white spruces on the perimeter of the burn (Werner and Post 1985; K. E. Post, unpublished data). Egg-laying by wood-boring beetles occurred at high densities only immediately after the fire, and we observed no secondary outbreaks in our

study area when adults from the 1983 cohort emerged in 1985 and 1986.

In contrast, three-toed woodpeckers fed primarily on larvae of scolytid beetles. Spruce beetles (*Dendroctonus rufipennis*) and other scolytids often respond dramatically to fire, attacking trees weakened or killed by fire (Muona and Rutanen 1994). Scolytids are considerably smaller than cerambycids; for example, mature larvae of the spruce beetle are about 6 mm long. In our study area, larval galleries of the spruce beetle and other scolytids (primarily *Ips* spp.) were abundant under the uncharred bark of lightly to moderately fire-damaged spruces, beginning the summer of the fire and for the next 2–3 years, until larvae from the 1983 cohort emerged as adults (Werner and Post 1985). Within our study area, there were no major secondary outbreaks of scolytids following emergence of the 1983 cohort.

Although our collections of foraging woodpeckers were limited, our observations of numbers, foraging sites, and foraging behaviors of black-backed and three-toed woodpeckers corroborate dietary differences suggested from those samples. Black-backed woodpeckers declined as adult white-spotted sawyers from the 1983 cohort first emerged in 1985, and black-backed woodpeckers disappeared once the remaining adults emerged in 1986. Primary foraging substrates of black-backed woodpeckers were moderately to heavily burned trees where only the white-spotted sawyer was abundant (Werner and Post 1985). Although we categorized only burn severity of foraging trees and not bark condition of foraging sites themselves, our qualitative observations indicated black-backed woodpeckers almost always foraged on portions of fire-damaged spruces where the bark was charred (and closely matched their sooty-black dorsal plumage). They also predominantly excavated, the only effective foraging

mode to extract wood-boring larvae from the sapwood. On heavily scorched spruces, abundance of cerambycid eggs was initially low and larval survival was poor because the sapwood quickly desiccated (R. A. Werner, Institute of Northern Forestry, personal communication), which would account for (1) earlier disappearance from the study area by female black-backed woodpeckers, who fed on more heavily burned substrates; (2) the shift by males to less-burnt trees in 1985–86 within the study area; and (3) infrequent occurrence of either sex in the interior of the burn where the spruces were killed immediately and severely scorched by the fire.

Three-toed woodpeckers mostly fed on uncharred portions of lightly to moderately burned spruces and primarily flaked and pecked, excavating only within the bark and cambium (also see Bull et al. 1986, Villard 1994). Thus, three-toed woodpeckers predominantly fed at sites where scolytid beetle larvae were most abundant (Werner and Post 1985) and used foraging modes (pecking, flaking) that were most effective in removing the bark and exposing the scolytid larval galleries.

Our findings of contrasting specialization of black-backed woodpeckers on cerambycids and three-toed woodpeckers on scolytids apparently contradict previous accounts indicating no differences in diets of black-backed and three-toed woodpeckers. However, all references to foods of these 2 species can be traced to Beal (1911: 25), who noted “the two species are so similar in habits that they may be treated together,” and that wood-boring beetle larvae predominated in the diet. Scolytids were so uncommon in prey remains that Beal (1911) concluded they were taken only incidentally to wood-boring larvae. In their first summer, first-instar larvae of both wood-boring and bark beetles live in the cambium, but wood-borers then enter the sapwood where they live until pupating and emerging as adults 2–3 summers later (Holsten et al. 1980, Post 1984). In contrast, bark beetles infesting conifers live only in the bark and cambium and never penetrate the sapwood (Werner et al. 1977, Stark 1982). Thus, the sites occupied by wood-boring and bark beetles potentially coincide only briefly, in the first summer of their life cycles. Our results suggest Beal (1911) overemphasized not only the similarity in food habits of black-backed and three-toed woodpeckers but also the specialization of the

three-toed woodpecker on wood-boring larvae. Perhaps his specimens had been feeding on first-summer larvae in the cambium, but Beal provided no details of collection dates or sites. All cerambycids in the stomachs of the three-toed woodpeckers that we collected were first instars. Furthermore, three-toed woodpeckers respond dramatically to scolytid outbreaks (Yeager 1955, Baldwin 1960, Koplin 1969, Bull et al. 1986), which suggests scolytids are important and preferred foods. Thus, we believe the three-toed woodpecker should be considered a specialist on beetles, particularly scolytids, which occur only in the inner bark and cambium of spruces.

The Rosie Creek fire resulted in immediate outbreaks of wood-boring and bark beetles, and thus abundant food for black-backed and three-toed woodpeckers, respectively. Bark beetle outbreaks also occur frequently and extensively in the absence of fire. For example, the spruce beetle probably is the largest mortality factor on white spruces in Alaska (Beckwith et al. 1977); Werner et al. (1977) summarized several major outbreaks of 100,000 ha or more. Only the three-toed woodpecker appears to be abundant when the outbreaks are occurring (R. A. Werner, personal communication). However, in Oregon, Bull et al. (1986) recorded both black-backed and three-toed woodpeckers during an outbreak of the mountain pine beetle (*Dendroctonus ponderosae*). Quantification of numeric responses of black-backed and three-toed woodpeckers to outbreaks of spruce beetles in the absence of fire clearly is needed.

Although hairy woodpeckers (particularly males) were abundant in our study area 1 year after the fire (Fig. 1), we observed 5 or more individuals on only 2 subsequent surveys and observed foraging behavior of fewer hairy woodpeckers than either black-backed or three-toed woodpeckers. In Oregon, Bull et al. (1986) documented no distinguishable differences in foraging behaviors and habitats of black-backed and hairy woodpeckers; in comparison, three-toed woodpeckers fed more by scaling on dead trees. In our study, we rarely observed female hairy woodpeckers, and male hairy woodpeckers used the study area more sporadically than either black-backed or male three-toed woodpeckers. Although male hairy woodpeckers fed on somewhat more severely burned spruces than black-backed woodpeckers, they also fed on cerambycid larvae (Table 3; also see Villard

and Beninger 1993). However, we observed hairy woodpeckers infrequently, and the degree of foraging overlap between male hairy woodpeckers and both sexes of the black-backed woodpecker deserves further study. Black-backed and hairy woodpeckers are similar in body size, but anatomical differences suggest black-backed woodpeckers are better able to extract wood-boring insect larvae, whereas hairy woodpeckers are better climbers (Spring 1965).

Within species, there were pronounced sexual differences either in foraging ecology or abundance. Female black-backed woodpeckers fed higher on trees and on more heavily burnt spruces than males. In comparison to males, female hairy woodpeckers fed relatively little on spruces and seldom excavated. Similar sexual differences in foraging ecology of hairy woodpeckers have been documented previously (Kilham 1965, Otvos and Stark 1985). Although male three-toed woodpeckers were abundant in the study area, particularly in 1984–85, we observed few female three-toed woodpeckers, which suggests females were spatially segregated from males. These results contrast sharply with Hogstad's (1976, 1977, 1978, 1991) intensive studies of three-toed woodpeckers in Eurasia, where substantial differences in morphology and foraging ecology of males and females permit sharing of territories. Hogstad (1993) attributed intersexual niche differentiation and spatial overlap of males and females in the three-toed woodpecker in Eurasia to lack of congeneric competitors. In contrast, the three-toed woodpecker co-occurs with several other *Picoides* species throughout its range in North America. Therefore, perhaps intersexual foraging competition is higher, and spatial overlap of males and females consequently less, in North America than in Eurasia.

All previous studies of the numerical responses of woodpeckers to fire have examined densities within burns (e.g., Hutto 1995). Although we did not systematically survey the central portions of the Rosie Creek burn, we frequently walked through them and did not find woodpeckers. The Rosie Creek fire produced favorable microenvironments only on its perimeter for both wood-boring and bark beetles; most spruces in the interior of the burn were killed immediately by the fire and were heavily scorched, providing unsuitable microhabitats for beetles (Werner and Post 1985), and thus woodpeckers. We believe edges of

stand-replacement fires represent a distinct and important habitat that future studies should distinguish from the interiors of burns.

We have suggested the black-backed woodpecker may be highly specialized in its foraging ecology and diet (also see Hutto 1995). Such specialization would be exceptional but not unique for woodpeckers. In Eurasia, the white-backed woodpecker (*Dendrocopos leucotos*) specializes on wood-boring insect larvae in deciduous trees and is threatened or endangered throughout much of its range (Virkkala et al. 1993, Hogstad and Stenberg 1994).

The Demography of the Black-Backed Woodpecker

Hutto (1995) proposed the black-backed woodpecker is basically restricted to early post-fire coniferous forests and that populations of this species are maintained by patchworks of recently burned forests. He further suggested the rarity of this species in unburned forests may indicate unburned forests are sink habitats where persistence is due to emigration from burns when conditions become less suitable several years after a fire. He concluded that the current lack of detailed studies of movement patterns and demography precluded resolution of this issue.

In our study area, densities observed on surveys were as high as 0.25 individuals/ha (Fig. 1), an order of magnitude above the mean density of 0.02 individuals/ha in 33 recently burned forests in the northern Rocky Mountains (Hutto 1995). Thus, the Rosie Creek fire represented an unparalleled opportunity for quantifying demography and movement patterns. However, the few nest sites we found in our study were inaccessible, and adults proved nearly impossible to trap; thus, it is highly unlikely that future study will provide sufficient data to quantify breeding success and survival in recently burned forests. Quantification of fecundity and survival in mature spruce forests is far more problematic simply because the species is so rare there; certainly densities are several orders of magnitude lower in mature spruce forests of Alaska than we documented in our study area immediately after a stand-replacement fire. Even sightings of black-backed woodpeckers have been extremely rare in Alaska (Gabrielson and Lincoln 1959). Thus, neither quantification of vital rates in putative source and sink habitats nor documentation of movement between them

is likely in the foreseeable future. Therefore, because future study likely will not quantitatively address this question, we provide a conceptual model here.

In Alaska, several sightings have confirmed the black-backed woodpecker does inhabit and can breed successfully in unburned spruce forests (J. M. Wright, Alaska Department of Fish and Game, personal communication). Throughout its geographic range, the black-backed woodpecker certainly is far more abundant in recent burns than in mature coniferous forests (Heinselman 1973, Niemi 1978, Apfelbaum and Haney 1981, Villard and Beninger 1993, Villard 1994, Hutto 1995), and this species clearly recruits to burns (Blackford 1955, our study). Indeed, Villard and Schieck (1996) documented nesting in a burn immediately after a fire had occurred.

Because black-backed woodpeckers so readily recruit to burns, we assume fitness is higher in burns than mature coniferous forests (see Fretwell 1972). We thus assume population size will increase ($\lambda_b > 1$), due to higher survival or reproduction, for the 2–3 years the species occupies a burn (b). If fires that result in outbreaks of wood-boring beetles are sufficiently frequent, black-backed woodpeckers could “island-hop” from 2–3-year-old burns to younger burns, exploiting 1 high-quality habitat patch after another (also see Hutto 1995). Certainly, fires are common and often extensive in boreal forests (Barney 1971, Rowe and Scotter 1973, Viereck 1973, Hunter 1993). For example, in 1940–79, lightning and human-caused forest fires burned an average of 306,702 ha/year in Interior Alaska (Gabriel and Tande 1983). However, annual variability in numbers and extent of fires is high; for example, only 1,389 ha burned in Interior Alaska in 1964, the lowest during the 1940–79 period (Gabriel and Tande 1983). In addition, many fires may not induce outbreaks of wood-boring beetles (R. A. Werner, personal communication), so that black-backed woodpeckers likely must alternate between occupying recent burns and unburned forests.

We consider 2 alternatives for population trajectories in unburned (u) forests. First, perhaps populations in unburned stands remain stationary ($\lambda_u = 1$); second, perhaps populations in unburned stands slowly decline ($\lambda_u < 1$). The first alternative (Fig. 4A) is unlikely, because the population would vacillate between phases of

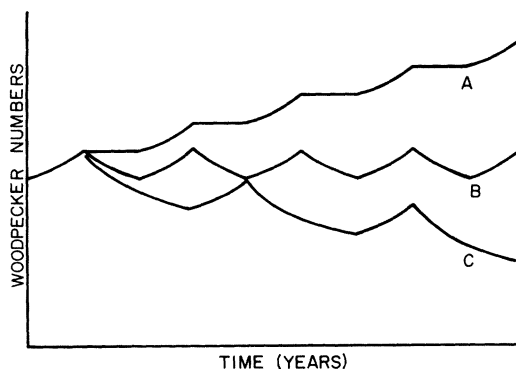


Fig. 4. Hypothetical population trajectories for black-backed woodpeckers alternating between occupation of burned (b ; periods of increase, $\lambda_b > 1$) and unburned (u) forests. (A) Population stationary during occupation of unburned forest, $\lambda_u = 1$. (B) Population declining during occupation of unburned forest, $\lambda_u < 1$. (C) Effect of doubling duration of periods in unburned forests, relative to B.

increase while in recent burns and stability while in unburned forests (i.e., the population would not remain rare). The second alternative seems more plausible: the population increases when recent burns are occupied and decreases when only unburned forests are occupied (Fig. 4B).

Thus, we view the frequency of fires within the dispersal range of individuals as a key determinant of population persistence (also see Thomas 1994, Hutto 1995). If fires are infrequent, the duration of periods of population decline will be increased (Fig. 4C). Conversely, fires not only can create preferred habitat (areas of wood-borer outbreaks), but they also can destroy secondary habitat (unburned spruce forest). For example, the perimeter of the Rosie Creek burn, where we documented high densities of black-backed and other woodpeckers, was only a small fraction of the 3,500-ha burn. Thus, very frequent or large fires also could be detrimental.

Movement of woodpeckers to new burns likely depends not only on the habitat suitability of the new burn relative to the present habitat (e.g., Fretwell 1972), but also the ability of the birds to detect and move to the new burn. These factors would be difficult to quantify effectively. However, black-backed woodpeckers obviously are capable of moving long distances, even though they are typically sedentary. Indeed, “invasions” of black-backed woodpeckers into southeastern Canada and the northeastern United States have been documented repeatedly (Van Tyne 1926, West and Speirs 1959, Yu-

nick 1985). The invasion in autumn 1923 came at the end of a several-year period of "almost inconceivable abundance" (J. M. Swaine, personal communication to Van Tyne) of wood-boring beetles (*Monochamus* spp.) and bark beetles within their normal range.

MANAGEMENT IMPLICATIONS

Currently, there is considerable interest in intensive logging of mature white spruce stands in Alaska, which would reduce secondary habitat where black-backed woodpeckers occur at very low densities. Salvage logging of insect-infested spruces is considered a necessary management practice. The intent of salvage logging after fire is to harvest and process the logs before wood-borer activity reduces the commercial value of the wood (e.g., Sampson et al. 1985). Consequently, salvage logging is designed to preclude or halt wood-borer outbreaks. Salvage logging therefore reduces or eliminates high-quality habitat for black-backed woodpeckers. If our conceptual model above is correct, maintaining viable populations of black-backed woodpeckers likely will necessitate delay of salvage logging until several years after fire (also see Hutto 1995). Although fire suppression is often limited in Alaska, it also precludes the generation of highly suitable habitat for black-backed woodpeckers. Thus, both fire suppression and salvage logging after fires will prolong periods of use of unburned spruce forests by black-backed woodpeckers and likely will cause black-backed woodpeckers to decline (see Fig. 4C vs. 4B).

Management practices to maintain old growth and prevent the types of fires that result in heavy infestations of wood-boring beetles will likely suppress numbers of black-backed woodpeckers and other similarly specialized species. Focusing on a single species (e.g., the spotted owl [*Strix occidentalis*] in the northwestern United States) is seen by some as an effective means of maintaining biodiversity (e.g., Adkisson 1988, Eisner et al. 1995). However, suppressing fires to maintain the spotted owl's habitat in those portions of its range where the black-backed woodpecker also occurs could eliminate the black-backed woodpecker (also see Hutto 1995). Conversely, the black-backed woodpecker likely has benefited by reintroduction of fire to enhance habitat for the Kirtland's warbler (*Dendroica kirtlandii*) in Minnesota (Mayfield 1958). While we would like to en-

courage consideration of delaying salvage logging to allow wood-boring beetle outbreaks to run their course and enhance habitat for black-backed woodpeckers, such a single-species focus should not be overdone. Certainly, the black-backed woodpecker benefits from fire and insect outbreaks that may be catastrophic for other species of wildlife (Rotenberry et al. 1995).

ACKNOWLEDGMENTS

We greatly appreciate the aid of G. C. Stevens, who identified prey remains, and the insights of R. A. Werner on the population dynamics of wood-boring and bark beetles during the course of our study. G. P. Juday helped secure funding for the project. R. N. Conner and J. Walters provided helpful critiques of an earlier version of this manuscript.

LITERATURE CITED

- ADKISSON, C. S. 1988. Cavity-nesting birds of North America: past history, present status, and future prospects. Pages 85–100 in J. A. Jackson, editor. Bird conservation. Volume 3. University of Wisconsin Press, Madison, Wisconsin, USA.
- AMMAN, G. D., AND P. H. BALDWIN. 1960. A comparison of methods for censusing woodpeckers in spruce–fir forests of Colorado. *Ecology* 41:699–706.
- APFELBAUM, S., AND A. HANEY. 1981. Bird populations before and after wildfire in a Great Lakes pine forest. *Condor* 83:347–354.
- BALDWIN, P. H. 1960. Overwintering of woodpeckers in bark beetle-infested spruce–fir forests of Colorado. *Proceedings of the International Ornithological Congress* 12:71–84.
- BARNEY, R. J. 1971. Wildfires in Alaska—some historical and projected effects and aspects. Pages 51–59 in C. W. Slaughter, R. J. Barney, and G. M. Hansen, editors. Fire in the northern environment—a symposium. U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.
- BEAL, F. E. 1911. Food of the woodpeckers of the United States. U.S. Department of Agriculture Biological Survey Bulletin 37.
- BECKWITH, R. C., J. O. WOLFF, AND J. C. ZASADA. 1977. Bark beetle response to clearcut and shelterwood systems in Interior Alaska after whole tree logging. U.S. Forest Service Research Note PNW-287.
- BENT, A. C. 1939. Life histories of North American woodpeckers. Smithsonian Institution, United States National Museum Bulletin 174.
- BLACKFORD, J. L. 1955. Woodpecker concentrations in burned forest. *Condor* 57:28–30.
- BOCK, C. E., AND J. H. BOCK. 1974. On the geographical ecology and evolution of the three-toed woodpeckers, *Picoides tridactylus* and *P. arcticus*. *American Midland Naturalist* 92:397–405.

- BULL, E. L., S. R. PETERSON, AND J. W. THOMAS. 1986. Resource partitioning among woodpeckers in northeastern Oregon. U.S. Forest Service Research Note PNW-444.
- CODY, M. L. 1974. Competition and the structure of bird communities. Princeton University Press Monographs in Population Biology 11.
- CONNELL, J. H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199:1302–1310.
- CONNER, R. N. 1979. Seasonal changes in woodpecker foraging methods: strategies for winter survival. Pages 95–105 in J. G. Dickson, R. N. Conner, R. R. Fleet, J. C. Kroll, and J. A. Jackson, editors. The role of insectivorous birds in forest ecosystems. Academic Press, New York, New York, USA.
- CONOVER, W. J. 1980. Practical nonparametric statistics. Second edition. John Wiley & Sons, New York, New York, USA.
- EISNER, T., J. LUBCHENCO, E. O. WILSON, D. S. WILCOVE, AND M. J. BEAN. 1995. Building a scientifically sound policy for protecting endangered species. *Science* 268:1231–1232.
- FLANNIGAN, M. D., AND B. M. WOTTON. 1991. Lightning-ignited forest fires in northwestern Ontario. *Canadian Journal of Forest Research* 21:277–287.
- FRETWELL, S. D. 1972. Populations in a seasonal environment. Princeton University Press Monographs in Population Biology 5.
- GABRIEL, H. W., AND G. F. TANDE. 1983. A regional approach to fire history in Alaska. Bureau of Land Management Technical Report 83/09.
- GABRIELSON, I. N., AND F. C. LINCOLN. 1959. The birds of Alaska. Wildlife Management Institute, Washington, D.C., USA.
- HEINSELMAN, M. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area. *Quaternary Research* 3:329–382.
- HOGSTAD, O. 1976. Sexual dimorphism and divergence in winter foraging behaviour of three-toed woodpeckers *Picoides tridactylus*. *Ibis* 118:41–50.
- . 1977. Seasonal change in intersexual niche differentiation of the three-toed woodpecker *Picoides tridactylus*. *Ornis Scandinavica* 7:101–111.
- . 1978. Sexual dimorphism in relation to winter foraging and territorial behaviour of the three-toed woodpecker *Picoides tridactylus* and three *Dendrocopos* species. *Ibis* 120:198–203.
- . 1991. The effect of social dominance on foraging by the three-toed woodpecker *Picoides tridactylus*. *Ibis* 133:271–276.
- . 1993. Why is the three-toed woodpecker (*Picoides tridactylus*) more sexually dimorphic than other European woodpeckers? Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg 67:109–118. (In English).
- , AND I. STENBERG. 1994. Habitat selection of a viable population of white-backed woodpeckers *Dendrocopos leucotos*. *Fauna Norvegica Series C, Cinclus* 17:75–94.
- HOLSTEN, E. H., R. A. WERNER, AND T. H. LAURENT. 1980. Insects and diseases of Alaskan forests. U.S. Forest Service Alaska Region Report 75.
- HUNTER, M. L., JR. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation* 65:115–120.
- HUSTON, M. 1979. A general hypothesis of species diversity. *American Naturalist* 113:81–101.
- HUTTO, R. L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology* 9:1041–1058.
- JUDAY, G. P. 1985. Preface: the Rosie Creek fire and its research opportunities. Pages vii–ix in G. P. Juday and C. T. Dyrness, editors. Early results of the Rosie Creek Fire Research Project 1984. University of Alaska-Fairbanks Agricultural and Forestry Experiment Station Miscellaneous Publication 85-2.
- KILHAM, L. 1965. Differences in feeding behavior of male and female hairy woodpeckers. *Wilson Bulletin* 77:134–145.
- KOPLIN, J. R. 1969. The numerical response of woodpeckers to insect prey in a subalpine forest in Colorado. *Condor* 71:436–438.
- MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599–619.
- MATTHYSEN, E., T. C. GRUBB, JR., AND D. CIMPRICH. 1991. Social control of sex-specific foraging behaviour in downy woodpeckers, *Picoides pubescens*. *Animal Behaviour* 42:515–517.
- MAYFIELD, H. 1958. Nesting of the black-backed three-toed woodpecker in Michigan. *Wilson Bulletin* 70:195–196.
- MORRISON, M. L., AND K. A. WITH. 1987. Interseasonal and intersexual resource partitioning in hairy and white-headed woodpeckers. *Auk* 104:225–233.
- MUONA, J., AND I. RUTANEN. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. *Annales Zoologici Fennici* 31:109–121.
- NIEMI, C. J. 1978. Breeding birds of burned and unburned areas in northern Minnesota. *Loon* 50:73–84.
- OTVOS, I. S. 1965. Studies on avian predators of *Dendroctonus brevicornis* LeConte (Coleoptera: Scolytidae) with special reference to Picipidae. *Canadian Entomologist* 97:1184–1199.
- , AND R. W. STARK. 1985. Arthropod food of some forest-inhabiting birds. *Canadian Entomologist* 117:971–990.
- PETERS, W. D., AND T. C. GRUBB, JR. 1983. An experimental analysis of sex-specific foraging in the downy woodpecker, *Picoides pubescens*. *Ecology* 64:1437–1443.
- PIMM, S. L., AND J. W. PIMM. 1982. Resource use, competition, and resource availability in Hawaiian honeycreepers. *Ecology* 63:1468–1480.
- POST, K. E. 1984. Wood borer (Cerambycidae and Buprestidae) infestation, development and impact on wood quality in recently felled white spruce trees in the interior of Alaska. Thesis, University of Alaska Fairbanks, Fairbanks, Alaska, USA.
- RABENOLD, K. N. 1978. Foraging strategies, diversity, and seasonality in bird communities of Appalachian spruce-fir forests. *Ecological Monographs* 48:397–424.

- RICHMAN, A. D., AND T. PRICE. 1992. Evolution of ecological differences in the Old World leaf warblers. *Nature* 355:817–821.
- ROTBERRY, J. T., R. J. COOPER, J. M. WUNDERLE, AND K. S. SMITH. 1995. When and how are populations limited: the roles of insect outbreaks, fires and other natural disturbances. Pages 55–84 in T. E. Martin and D. M. Finch, editors. *Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues*. Oxford University Press, New York, New York, USA.
- , AND J. A. WIENS. 1980. Temporal variation in habitat structure and shrubsteppe bird dynamics. *Oecologia* 47:1–9.
- ROWE, J. S., AND G. W. SCOTTER. 1973. Fire in the boreal forest. *Quaternary Research* 3:444–464.
- SAMPSON, G. R., S. A. ERNST, AND F. A. RUPPERT. 1985. Lumber recovery of live and fire-killed white spruce. Pages 17–19 in G. P. Juday and C. T. Dyrness, editors. *Early results of the Rosie Creek Fire Research Project 1984*. University of Alaska-Fairbanks Agricultural and Forestry Experiment Station Miscellaneous Publication 85-2.
- SELANDER, R. K. 1965. Sexual dimorphism in relation to foraging behavior in the hairy woodpecker. *Wilson Bulletin* 77:416.
- SHORT, L. L. 1974. Habits and interactions of North American three-toed woodpeckers (*Picoides arcticus* and *Picoides tridactylus*). *American Museum Novitates* 2547.
- SPINDLER, M. A., AND B. KESSEL. 1980. Avian populations and habitat use in Interior Alaska taiga. *Syesis* 13:61–104.
- SPRING, L. W. 1965. Climbing and pecking adaptations in some North American woodpeckers. *Condor* 67:457–488.
- STARK, R. W. 1982. Generalized ecology and life cycle of bark beetles. Pages 21–45 in J. B. Mitton and K. B. Sturgeon, editors. *Bark beetles in North American conifers*. University of Texas Press, Austin, Texas, USA.
- THOMAS, C. D. 1994. Extinction, colonization, and metapopulations: environmental tracking by rare species. *Conservation Biology* 8:373–378.
- TÖRÖK, J. 1990. Resource partitioning among three woodpecker species *Dendrocopos* spp. during the breeding season. *Holarctic Ecology* 13:257–264.
- VAN TYNE, J. 1926. An unusual flight of the arctic three-toed woodpecker. *Auk* 43:469–474.
- VIERECK, L. A. 1973. Wildfire in the taiga of Alaska. *Quaternary Research* 3:465–495.
- VILLARD, P. 1994. Foraging behavior of black-backed and three-toed woodpeckers during spring and summer in a Canadian boreal forest. *Canadian Journal of Zoology* 72:1957–1959.
- , AND C. W. BENINGER. 1993. Foraging behavior of male black-backed and hairy woodpeckers in a forest burn. *Journal of Field Ornithology* 64:71–76.
- , AND J. SCHIECK. 1996. Immediate post-fire nesting by black-backed woodpeckers, *Picoides arcticus*, in northern Alberta. *Canadian Field-Naturalist* 111:478–479.
- VIRKKALA, R., T. ALANKO, T. LAINE, AND J. TIAINEN. 1993. Population contraction of the white-backed woodpecker *Dendrocopos leucotos* in Finland as a consequence of habitat alteration. *Biological Conservation* 66:47–53.
- WALLACE, R. A. 1974. Ecological and social implications of sexual dimorphism in five melanerpine woodpeckers. *Condor* 76:238–248.
- WERNER, R. A., B. H. BAKER, AND P. A. RUSH. 1977. The spruce beetle in spruce forests of Alaska. U.S. Forest Service General Technical Report PNW-61.
- , AND K. E. POST. 1985. Effects of wood-boring insects and bark beetles on survival and growth of burned white spruce. Pages 14–16 in G. P. Juday and C. T. Dyrness, editors. *Early results of the Rosie Creek Fire Research Project 1984*. University of Alaska-Fairbanks Agricultural and Forestry Experiment Station Miscellaneous Publication 85-2.
- WEST, J. D., AND J. M. SPEIRS. 1959. The 1956–1957 invasion of three-toed woodpeckers. *Wilson Bulletin* 71:348–363.
- WICKMAN, B. E. 1965. Black-backed three-toed woodpecker, *Picoides arcticus*, predation on *Monochamus oregonensis*. *Pan-Pacific Entomologist* 41:162–164.
- WILLIAMS, J. B., AND G. O. BATZLI. 1979. Competition among bark-foraging birds in central Illinois: experimental evidence. *Condor* 81:122–132.
- YEAGER, L. E. 1955. Two woodpecker populations in relation to environmental change. *Condor* 57:148–153.
- YUNICK, R. P. 1985. A review of recent irruptions of the black-backed woodpecker and three-toed woodpecker in eastern North America. *Journal of Field Ornithology* 56:138–152.

Received 10 February 1997.

Accepted 10 March 1998.

Associate Editor: Lutz.